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KLEPTOPARASITISM BY SOUTH POLAR SKUAS ON BLUE-EYED SHAGS IN ANTARCTICA

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Kleptoparasitism, or piracy, is widespread among the Laridae and Stercorariidae (see Brockmann and Barnard 1979, for review). While several studies have quantified the parasitism of Great Skuas (*Catharacta skua*) on a number of North Atlantic seabirds (Meinertzhagen 1959, Andersson 1976, Furness 1978, Arnason and Grant 1978), only anecdotal accounts have treated the subject for Chilean Skuas (*C. chilensis*) and South Polar Skuas (*C. maccormicki*) (Murphy 1936, Holdgate 1963, Burton 1968, Watson 1975).

We casually observed 50–100 chases of Blue-eyed Shags (*Phalacrocorax atriceps*) by South Polar Skuas at Palmer Station, Antarctica from mid-December 1978 to early February 1979. Although some chases involved physical attacks on flying shags, only once did a shag regurgitate food. Since chases often covered distances of 500 m or more, this seemed an energetically expensive foraging technique so we investigated it in detail during austral summer 1979–80. Our objectives were: (1) to determine methods of attack by skuas and response to attack by shags; (2) to determine whether chases were more frequent near to (<1 km) or away from (3.5–7 km) the shag colony; (3) to determine whether environmental factors contributed to the number and success of chases; (4) to estimate whether kleptoparasitism is energetically profitable for skuas; and (5) to compare chase success of South Polar Skuas with that of other skuas, jaegers (*Stercorarius* spp.) and gulls (*Larus* spp.) which pirate food by means of aerial pursuits.

STUDY AREA AND METHODS

The study was conducted from 28 October 1979–11 March 1980, in the vicinity of Palmer Station, Anvers Island (64°46′S, 64°03′W) near the Antarctic Peninsula (Fig. 1). During our study pack-ice cover of the ocean (Fig. 1) varied from 0–100%, changing daily depending on wind direction and velocity, and tidal currents.

A variety of seabirds nest on exposed peninsulas projecting from glacier-covered Anvers Island and on equally exposed small rocky islands nearby (Parmelee et al. 1977). Breeding Brown Skuas (*C. lonnbergi*) were outnumbered by breeding South Polar Skuas approximately 25:1 but typically held territories near Adélie Penguin (*Pygoscelis adeliae*) colonies from which they excluded the smaller south polars. South Polar Skuas nested on virtually all islands and ice-free peninsulas near Palmer Station (Fig. 1), and a minimum of 241 pairs successfully hatched chicks during 1979–80. An undetermined number of nonbreeders and/or failed breeders were also present and gathered in groups of up to 90 at a glacial melt pond near the base of Norsel Point and on Christine Island. The only Blue-eyed Shag colony within

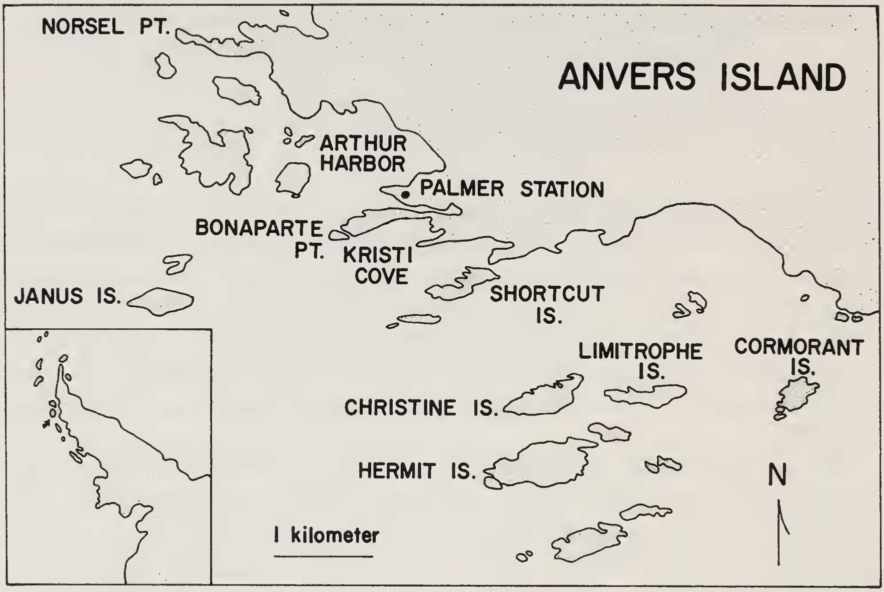

FIG. 1. Palmer Station, Antarctica and vicinity. (Arrow in inset indicates location of Anvers Island relative to the Antarctic Peninsula.)

15 km of Palmer Station is on Cormorant Island where nest counts totaled 485 (31 December 1978) and 326 (19 December 1979).

Scheduled observations were carried out from two locations—atop the shag colony on Cormorant Island facing northwest and near the base of Bonaparte Point (4 km from the colony) facing southwest. Each site afforded approximately a 1 km^2 view of an area through which shags frequently travelled.

During observation periods lasting 3–24 h, we recorded weather and pack ice conditions, the number of shags flying toward the colony, the number of shags flying away from the colony, the number of chases by skuas, the number of skuas involved in chases, attack methods of skuas, response to attack by shags, and the number of regurgitations by shags. We also recorded all other chases of shags whenever observed.

RESULTS

Breeding phenology.—Blue-eyed Shags are present in the Palmer area year round and often remain at the breeding colony during the winter (Holdgate 1963; Glass 1978; Bernstein and Maxson, unpubl.). During the 1979–80 season, courtship, pairing and nest-building began in September; egg-laying occurred early November to mid-December; hatching began in early December; and chicks were attended and fed by both parents from hatch to March. Time budget data indicate that each parent foraged once per day while the other remained at the nest. As chicks neared fledging in mid-February, both parents often foraged simultaneously.

South Polar Skuas returned to the study area in mid-November. Egg-laying ranged from mid-January through mid-February. When we departed the study area on 11 March, a few older chicks were fledging but many others were still in the downy stage (Pietz and Maxson, unpubl.).

Qualitative aspects of chases.—A common flight path for shags returning to the colony was south across Arthur Harbor, over or around Bonaparte Point, southwest across Kristi Cove and through the narrow gap between Shortcut and Anvers islands (see Fig. 1). Sixteen and 19 pairs of South Polar Skuas nested on Bonaparte Point and Shortcut Island, respectively, making Kristi Cove an area of potentially numerous skua-shag interactions.

Shags approached Cormorant Island from all directions but most often from the west or northwest. Six pairs of South Polar Skuas occupied breeding territories on Cormorant Island during 1979–80, although only two of these produced eggs. A total of 107 pairs of skuas bred on nearby Limitrophe, Christine, and Hermit islands from where they could readily harass shags flying to and from the colony.

Skuas attempted to induce shags to regurgitate by aerial harassment. Being faster, more aerobatic flyers, skuas readily overtook and outmaneuvered shags in most situations. Sometimes skuas simply flew close behind a shag or swooped at it, but often they attacked the shag by biting at its back, rear, or belly. If a shag regurgitated, the skua caught the fish in mid-air or retrieved it from the water.

Shags responded to chases in several ways. Single shags or small groups often swerved away from an approaching skua in turns of up to 180°. This maneuver was sometimes successful in ending a chase. Larger groups of shags (10–20) rarely turned away and remained in formation until attack was imminent. Then the flock typically split into smaller units flying different directions whereupon the skua focused on one group or an individual and continued the chase. If the flock was large (>30), attack by a single skua did not result in fragmentation of the flock but merely perturbations in the immediate vicinity of the attacker.

The most effective evasive action by shags was landing on the water, though they did not actually land until skuas struck them or were about to strike. Occasionally a skua attempted to prevent its victim from landing by flying beneath it and biting at its belly even when the shag was only 2 m above the surface, but a shag in this position was still able to land if open water was available.

If shags reached the water without regurgitating, skuas often gave up. Persistent skuas, however, swooped at the shag. Shags responded by either jumping up and biting at the skua or by diving. In the latter case, the skua either flew off, hovered overhead, or landed on an ice floe until the shag

TABLE 1

SUMMARY OF SCHEDULED OBSERVATIONS AT SHAG COLONY AND AT KRISTI COVE 4 KM FROM COLONY

		Shags flying toward colony			
Observation site	No. h	No. shags	No. chases	% chased	No. regurg.
Cormorant Island	72	1684	4	0.2	0
Kristi Cove	93	726	71	9.8	2

	Shags flying away from colony				
	No. shags	No. chases	% chased	No. regurg.	Chases per h
Cormorant Island	1384	1	0.1	0	0.1
Kristi Cove	895	21	2.3	0	1.0

surfaced, whereupon the skua swooped again. This tactic was never observed to be successful, although Murphy (1936) did observe skuas snatching fish from shags as they surfaced from a foraging dive.

Quantitative aspects of chases.—Scheduled observations totaled 165 h (Table 1). Although more shags were observed near the colony than at Kristi Cove, they were attacked less often ($\chi^2 = 159.2$, df = 1, $P < 0.001$). At Kristi Cove shags were chased more often when flying toward than when flying away from the colony ($\chi^2 = 41.3$, df = 1, $P < 0.001$).

During scheduled observations, no shags within 1 km of the colony (Table 1) were induced to regurgitate fish. Two birds arriving with nest material (aquatic vegetation) dropped the vegetation when chased, but the skuas made no attempt to retrieve these items. At Kristi Cove no pursuits of shags flying away from the colony were successful and only two (2.5%) chases of shags flying toward the colony resulted in regurgitation.

Overall, we observed 280 chases of which 13 (4.6%) resulted in regurgitation (Table 2). Although time spent at Cormorant Island was roughly equivalent to time in the field at other locations and despite nearly equal chase success rates near and away from the colony, only 27 (9.6%) chases were witnessed at the colony. The majority (73%) of pursuits (and all successful chases) were of shags flying toward the colony. Skuas were unsuccessful when chasing shags flying away from the colony or when swooping at swimming shags.

To investigate factors that potentially influence chase success we categorized chases (3.5–7 km from the colony) relative to the numbers of shags and skuas involved (Table 3). Success rate for single skuas chasing lone shags was 4.6%, and no increase in success was evident when several

TABLE 2
CHASE SUCCESS RELATIVE TO SHAG BEHAVIOR AND CHASE LOCATION

	3.5–7 km from colony			<1 km from colony		
	No. chases	Successful No.	Successful %	No. chases	Successful No.	Successful %
Shags flying away from colony	47	0	0.0	6	0	0.0
Shags flying toward colony	188	12	6.4	16	1	6.2
Shags swimming	18	0	0.0	5	0	0.0
Total	253	12	4.7	27	1	3.7

skuas pursued a single shag or when one skua pursued a group of shags. We observed groups of two to ten skuas ($\bar{x} = 3.9 \pm 3.1$) pursuing groups of shags. These multiple pursuits resulted in a four-fold increase (to 21%) in the probability that at least one shag would regurgitate. However, skuas in these groups were clearly acting as individuals and when the flocks split up, each typically pursued a different shag. When success rate per skua was calculated for these groups there was no increase in success.

In 68 chases where skuas did not strike any of the birds pursued, only 5 of 227 shags (2.2%) regurgitated, but in 32 of these chases skuas gave up before closing within striking distance. Of 64 chases where skuas struck shags, eight (12.5%) resulted in regurgitations (Table 4). Most often skuas flew immediately behind shags and bit at their tail area. The data suggest, however, that greater success was achieved when a skua flew beneath a shag and bit upwards at the shag's belly.

Influence of environmental factors.—Although our study spanned 136 days, 12 of the 13 observed regurgitations occurred between 13–15 December. At 17:00, 13 December, we noted an unusual number of chases. From atop one of the Palmer Station buildings we observed the Arthur Harbor and Kristi Cove areas (approx. 2 km^2) until 18:45, recording 38 chases with

TABLE 3
CHASE SUCCESS RELATIVE TO NUMBER OF SKUAS AND SHAGS INVOLVED

No. shags	No. skuas	No. chases	No. regurgitations	% success/ chase	% success/ skua
1	1	43	2	4.6	4.6
1	>1	7	0	0.0	0.0
>1	1	36	2	5.5	5.5
>1	>1	38	8	21.0	5.3

TABLE 4
SUMMARY OF CHASES WHERE SKUA STRUCK SHAG

Where struck	No.	No. regurgitations	% success
Rear	37	4	10.8
Back	6	0	0.0
Belly	15	4	26.7
Back and belly	6	0	0.0
Total	64	8	12.5

eight regurgitations. The chase rate of 22/h was much greater than that observed during any of the scheduled watches (Table 1). All five instances of shags regurgitating without first being struck occurred during this 1.7-h period. Most regurgitated as the skua approached closely and appeared about to strike but one bird regurgitated to a skua which was flying well below it and still about 20 m away.

The environmental factor common to all instances of successful chases (including the one observed during the 1978–79 season) was the presence of dense pack ice, which influenced the number and success rate of chases in two ways. First, shags were more vulnerable at this time because lack of open water areas precluded their most effective means of escape (shags are not maneuverable fliers and have difficulty landing in small patches of open water between ice floes, particularly when their flight is being disrupted by a skua). When unable to find a suitable landing site, the surest way for a shag to rid itself of a pursuing skua was to regurgitate a fish. Second, South Polar Skuas near Palmer Station were primarily dependent on the sea for food since Brown Skuas controlled penguin colonies and edible garbage from the station was sealed in metal barrels. Consequently, when dense pack ice stretched to the horizon (a situation not uncommon during the breeding season [Parmelee et al. 1978]) skuas had to fly long distances to find open water areas where they could capture fish or krill. As an alternative, they could remain near their territories and increase their efforts to steal food from shags.

Support for these hypotheses is presented in Table 5. On 8 December the pack ice was 1–2 km away from the shore of Anvers Island leaving large areas of ice-free water. In contrast, the pack ice on 14 December covered over 95% of the area extending from the shore of Anvers Island to the horizon. Although many shags flew across Kristi Cove on both days, significantly more chases occurred ($\chi^2 = 43.4$, df $= 1$, $P < 0.001$) when the pack ice was in. The same pattern is indicated by increases in the

TABLE 5
INFLUENCE OF PACK ICE ON CHASE FREQUENCY AND SUCCESS DURING TWO 24-H SCHEDULED OBSERVATIONS AT KRISTI COVE

Date	Pack ice	No. shags	No. chases	% chased	No. regurgitations	Chases/h
8 Dec.	Out	681	9	1.3	0	0.4
14 Dec.	In	661	62	9.4	2	2.6

percentage of shags chased and in the number of chases per hour from 8–14 December.

Further evidence is that all pack ice blew out to sea during a storm on 9–10 January 1980, leaving the Palmer Station area largely ice free through the end of the breeding season. Only 8 (none successful) of 280 total chases observed occurred after 9 January, although food demands for both skuas and shags peaked after that date due to food requirements of chicks.

DISCUSSION

Factors influencing chase success.—An obvious influence on chase success is whether a shag is carrying food. A bird leaving the colony to forage probably has little or no food in its stomach and no chases of shags flying away from the colony were successful (Tables 1, 2). Likewise, a bird returning to the colony after foraging has a high probability of carrying food. Successful kleptoparasites would be expected to discriminate between the two groups. This appears to be the case, as 73% of chases (Table 2) as well as the higher proportion of shags chased (Table 1) were birds flying toward the colony. Cues skuas used to distinguish the two groups (even at distances of 7 km from the colony) remain unknown as there were no visual differences in flight speed or body contour apparent to us. Perhaps skuas have learned to associate food with the shags' flight direction simply through trial and error chases of both groups.

Increasing the number of pursuers usually increases chase success while decreasing individual success (Hatch 1970, 1975; Grant 1971; Andersson 1976; Hulsman 1976; Verbeek 1977; Arnason and Grant 1978; Taylor 1979). In the present study, chase success increased from about 5% when single skuas chased either individuals or groups of shags to 21% when groups of skuas chased groups of shags (Table 3). Success per individual, however, remained near 5%. Whereas other workers typically report multiple chases of individuals, we most often observed multiple chases of groups which became several individual chases after shag flocks divided.

Andersson (1976) reported that pursued Northern Gannets (*Sula bas-*

sana) were no more likely to regurgitate when struck by Great Skuas than when untouched. In contrast, we found that 8 of 64 (12.5%) shags struck during chases regurgitated (Table 4), whereas only 5 of 227 (2.2%) shags not struck did so.

Dense pack ice influenced the number of chases by making the skuas' primary food (fish and krill) more difficult to obtain and influenced chase success by making it difficult for shags to escape skuas by landing on the water. All observed regurgitations occurred under these conditions. Similarly, at a colony where Common Puffins (*Fratercula arctica*) had to fly 1 km over land before reaching the nesting cliffs and could not readily escape to the sea, Parasitic Jaegers (*Stercorarius parasiticus*) achieved high chase success (51–69%) (Grant 1971, Arnason and Grant 1978) compared with success rates (15–22%) at colonies adjacent to the sea (Andersson 1976; Furness 1977, 1978).

Comparison with other kleptoparasites.—The Appendix compares chase success of South Polar Skuas with that of other skuas, jaegers, and gulls which engage in aerial pursuits of hosts. With the exception of two cases with 0% success (Furness 1977), which can be discounted due to very small sample sizes, the overall chase success of the present study is the lowest reported for this type of kleptoparasitism. All birds (except Herring Gulls [*Larus argentatus*] [Verbeek 1977]) achieving a success rate under 15% parasitized additional species at the same site which yielded higher success. At Palmer Station, Antarctic Terns (*Sterna vittata*), Southern Black-backed Gulls (*L. dominicanus*) and Southern Giant Fulmars (*Macronectes giganteus*) also bred and were potential hosts. In two seasons, however, we observed fewer than 10 chases of either terns or gulls and no chases of Giant Fulmars. Holdgate (1963) likewise reported that skuas confined most parasitic chases to shags in the Palmer Station area.

Profitability of kleptoparasitism to skuas.—In view of the low chase success observed, it is of interest to determine whether skuas achieve an energy profit through kleptoparasitism. While precise calculations are beyond the scope of this study, some energy cost/benefit approximations can be made. The mass-specific oxygen consumption of nine South Polar Skuas at Palmer Station was found to be 1.30 l O_2/kg/h ± 0.05 (R. Ricklefs, pers. comm.), a value nearly double that predicted by the equation of Lasiewski and Dawson (1967). Weights of 80 South Polar Skuas captured near the station averaged 1156 ± 98 g (Pietz and Maxson, unpubl.). Using these values the standard metabolic rate (SMR) of an average-weight skua is 29.6 kJ/h. At an average chase success of 4.6% (Table 2), a skua would require over 20 chases before causing a shag to regurgitate. Chases of 500 m were common and some continued for 1 km or more. Thus, to obtain one fish, a skua would likely have to fly a total of 10–20 km at top speed chasing shags, plus, perhaps a similar distance at energetically less costly flight while returning to its territory. Flight speed of Blue-eyed Shags was approximately 48 kmph (Bernstein and Maxson, unpubl.). If, for example, a skua flew 15 km at chase speeds of 60 kmph and returned at 40 kmph, and if chasing and returning cost 15.2 × SMR (King 1974) and 8 × SMR, respectively, the bird would expend roughly 201.3 kJ obtaining a fish.

Fish regurgitated to skuas were ca. 9–14 cm long. A fish of similar size (13.6 cm) regurgitated at the colony during shag banding operations weighed 40 g. Assuming that energy content of fish equals 1.14 Kcal/g (4.77 kJ/g) fresh weight (Dunn 1975) and that skuas have a digestive efficiency of 80% (Uramoto 1961, Kahl 1964, Dunn 1975, Kushlan 1977, Cooper 1978), a skua pirating a similar fish would obtain 152.6 kJ of metabolizeable energy. In the example above, the bird would suffer a net energy loss of 48.7 kJ. Clearly, variation in the above factors will alter the cost/benefit ratio, but these calculations suggest that it would be difficult for a skua to achieve any substantial energy profit at the low chase success rates observed.

No South Polar Skuas were known to rely on piracy as a major source of food during our study. For example, on 13 days between 8 December 1979–9 March 1980 P. Pietz and G. Maxson (unpubl.) conducted 265 h of scheduled observations on Bonaparte Point in which four pairs of color banded skuas were simultaneously observed for periods of 14–24 h. Only 14 chases (involving both sexes, none successful) by these banded skuas were observed and no individual was seen chasing shags more than three times in a single day. Probably other foods could predictably be obtained, at less expense, under most conditions.

We hypothesize that individual skuas chase shags, in part, to assess their vulnerability to kleptoparasitism. Skuas are opportunistic foragers, clearly aware of the activities of other skuas, and are quickly attracted to the discovery of an ephemeral food source. Regurgitation by shags and the subsequent retrieval of the fish by skuas are conspicuous activities. When shags prove vulnerable, chasing is likely to become contagious and could readily develop into the situation observed on 13 December. Thus, individual skuas would spend relatively little time or energy chasing under most circumstances but would increase their efforts when chasing proved energetically profitable.

SUMMARY

South Polar Skua (*Catharacta maccormicki*) kleptoparasitism on Blue-eyed Shags (*Phalacrocorax atriceps*) was studied at Palmer Station, Antarctica (64°46′S, 64°03′W) from 28 October 1979–11 March 1980. Skuas attempted to induce shags to regurgitate fish by means of aerial harassment. The shags' most effective means of escaping attack was landing on the water. Of 280 chases observed, only 13 (4.6%) were successful. This success rate is lower than that reported for other skuas, jaegers and gulls which pirate food through aerial pursuits of hosts. The majority of chases (73%) were of shags returning to their breeding colony, but most chasing occurred away from (3.5–7 km) the colony itself. Chase success increased to 21% when groups of skuas pursued groups of shags but success per skua remained near 5%. Skuas struck shags during 64 chases resulting in 8 (12.5%) regurgitations. In contrast, during 68 chases where no shags were struck, only 5 of 227 shags (2.2%) regurgitated. All successful chases occurred during periods of dense pack ice which left few areas of open water. Dense pack ice caused an increase in chasing because it made the skuas' primary food (fish and krill) more difficult to obtain. Lack of open water also increased chase success by making it more difficult for shags to find suitable landing sites to escape attack. Energy budget estimates suggest it is unlikely that skuas achieve an energy profit at the low success rates observed and no skuas were known to rely on piracy as a major food source during the study.

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APPENDIX

CHASE SUCCESS BY SKUAS, JAEGERS AND GULLS ENGAGING IN AERIAL PURSUITS OF HOSTS

Kleptoparasite	Host	No. chases	% successful	Source
South Polar Skua	Blue-eyed Shag	280	4.6	This study
Great Skua	Northern Gannet	11	100.0	Meinertzhagen 1959
		93	11.8	Andersson 1976
		69	30.4	Furness 1978
	Common Puffin	32	18.7	Andersson 1976
		233	37.7	Furness 1978
		32	34.4	Arnason and Grant 1978
	Black-legged Kittiwake (*Rissa tridactyla*)	13	15.4	Furness 1978
	Razorbill (*Alca torda*)	38	18.4	Furness 1978
	Common Murre (*Uria aalge*)	113	29.2	Furness 1978
Parasitic Jaeger	Common Puffin	88	21.6	Andersson 1976
		140	50.7	Grant 1971
		1101	68.8	Arnason and Grant 1978
		110	20.9	Furness 1978
		13	15.4	Furness 1977
	Arctic Tern (*Sterna paradisaea*)	87	43.7	Furness 1978
		220	47.7	Furness 1977
		70	40.0[a]	Taylor 1979
	Black-legged Kittiwake	33	33.3	Furness 1978
		16	25.0	Furness 1977
	Razorbill	18	11.1	Furness 1978
		3	0.0	Furness 1977
	Common Murre	27	11.1	Furness 1978
		3	0.0	Furness 1977
Parasitic Jaeger	Sandwich Tern (*Sterna sandvicensis*)	254	23.2[a]	Taylor 1979
	Common Tern (*S. hirundo*)	100	9.0[a]	Taylor 1979
Lesser Black-backed Gull (*Larus fuscus*)	Herring Gull	118	43.2	Verbeek 1977
	Lesser Black-backed Gull	86	20.9	Verbeek 1977

Appendix
Continued

Kleptoparasite	Host	No. chases	% successful	Source
Herring Gull	Herring Gull	10	10.0	Verbeek 1977
	Lesser Black-backed Gull	19	10.5	Verbeek 1977
Herring Gull–Lesser Black-backed Gull	Common Puffin	29	34.5	Arnason and Grant 1978
		15	26.6	Corkhill 1973
Black-legged Kittiwake	Common Puffin	7	42.9	Arnason and Grant 1978
Laughing Gull (*L. atricilla*)	Arctic Tern–Common Tern	87	78.2	Hatch 1970
Silver Gull (*L. novaehollandiae*)	Crested Tern (*S. bergii*)	711	16.7[a]	Hulsman 1976
	Lesser Crested Tern (*S. bengalensis*)	77	6.5	Hulsman 1976

[a] Original data recalculated to fit Appendix.